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Burke Museum Contributions in Anthropology and Natural History

No. 9



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A New Species of *Cancer* (Decapoda: Brachyura) from the Miocene Astoria Formation in Washington

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ABSTRACT

A new species of crab, *Cancer wahkiakumensis*, is described from fossils of early to early middle Miocene age in the Astoria Formation of southwestern Washington. These fossils were collected from rocks within a relatively small depositional basin within which the new taxon appears to have been endemic. Rocks of the Astoria Formation in southwestern Washington contain a very diverse crustacean assemblage including the families Atelecyclidae (?), Calappidae, Callianassidae, Cancridae, Galatheidae, and Majidae. Of these, only the Callianassidae has been previously identified from the Astoria Formation.

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INTRODUCTION

Rocks of the Astoria Formation in southwestern Washington contain fossils which represent a diverse and previously undocumented decapod crustacean assemblage. These fossils include species representing the families Atelecyclidae (?), Calappidae, Callianassidae, Cancridae, Galatheidae, and Majidae (table 1). There are, in addition, two crab species whose familial relationships are still to be determined, and at least three cancrid species whose identity must await the discovery of more complete specimens. This paper describes a new species of the genus *Cancer* from this fossil decapod assemblage.

Very few fossil decapods have been documented from rocks of the Astoria Formation, which is exposed throughout much of coastal Oregon and western Washington (Etherington 1931; Moore 1963). In Oregon, the mud-shrimp *Callianassa oregonensis* Dana, 1849, is the only decapod described from rocks of the Astoria Formation. In southwestern Washington, Rathbun (1926) identified *Callianassa clallamensis*, *C. twinensis*, and a crab, *Eumorphocorystes naselensis*, all from rocks now mapped as part of the Astoria Formation (Wolfe and McKee 1968, 1972; Wells 1979, 1989).

Figure 1.

Map of Grays River area of southwestern Washington showing place names and collecting localities. Rocks of the Astoria Formation crop out at the town of Grays River along a roadcut immediately southwest of the town and adjacent to the river. One of the paratypes of *Callianassa twinensis* Rathbun, 1926, was collected from "sandy shale bluffs on Grays River, at Grays River" (Rathbun 1926:117); however, during this investigation no additional specimens of *C. twinensis* were found at or near this locality. Claw parts tentatively identified as *C. twinensis* were collected at several localities along Salmon Creek (near Naselle) and along the north shore of the Columbia River, west of Rocky Point and east of the site of the town of Frankfort. Elsewhere, *C. twinensis* is known only from older sediments (Rathbun 1926).

Rathbun (1926) identified Callianassa clallamensis and described a raninid crab, Eumorphocorystes naselensis, from a locality near Naselle. This locality (Stanford University, North Pacific 281) is described as being along the Naselle River, near the mouth of Salmon Creek (Rathbun 1926:16). Rocks near the mouth of Salmon Creek have been mapped by Wells (1979, 1989) as part of the Astoria Formation of early Miocene age. Our efforts to confirm the presence of C. clallamensis and E. naselensis in rocks at that locality have been unsuccessful; however, C. clallamensis was found at several localities within the Astoria Formation along Salmon Creek, east of Naselle. Interestingly, Rathbun (1926:16) noted that the locality number for the holotype of E. naselensis was "badly rubbed but is almost certainly 281." The presence of E. naselensis in older rocks of the northeast Pacific basin (Jeletzky 1975;

Tucker and Feldmann 1990) and the apparent absence of this taxon in the Astoria Formation raises a question concerning the accuracy of the type locality description.

The mud-shrimps Callianassa clallamensis, C. oregonensis, and C. twinensis are, therefore, the only decapod crustaceans previously documented with certainty from rocks of the Astoria Formation.



DEPOSITIONAL SETTING AND PALEOECOLOGY

Rocks of the Astoria Formation are widely distributed in southwestern Washington (Weaver 1937; Wolfe and McKee 1968, 1972; Wells 1979, 1989) but these rocks are not well exposed because of thick vegetation. The formation is best exposed along streams and rivers, especially at a few localities along the north shore of the Columbia River, between the old townsite of Knappton on the west and Altoona to the east. Smaller outcrops are along the Naselle River, and Salmon Creek, near the town of Naselle.

Wolfe and McKee (1968, 1972) divided the Astoria Formation within the Grays River Quadrangle (U.S. Geological Survey, 15 minute series) into units I, II, and III. West of the Grays River Quadrangle, rocks of the Astoria Formation, including facies of units I and III, were named the Naselle unit and Bald Ridge unit, respectively, by Wells (1989). These rocks were deposited in a local downwarp, perhaps near the mouth

of the ancestral Columbia River (Wolfe and McKee 1972). The new cancrid crab has been found only in rocks of units I and II that were deposited within this small embayment.

Although the geology of the Astoria Formation has been examined and reported, the macropaleontology of the formation in southwestern Washington has not received much detailed attention. Weaver (1937, 1942) listed some fossil localities in the area; faunal lists (Foraminifera and mollusks) were given by Wolfe and McKee (1972); an otariid pinniped was described by Barnes (1987); and some new pteropods were described by Squires (1989). The molluscan fauna has been assigned to the Pillarian (early Miocene) and Newportian (early to early middle Miocene) provincial molluscan stages by Moore and Addicott (1987). The mollusks suggest warm marine conditions;

Foraminifera referable to the Saucesian Stage from units I and II indicate water depths ranging between approximately 30 and 150 meters (Wolfe and McKee 1972).

Fossil plants from rocks of unit III (Bald Ridge unit) suggest a warm climate on the adjacent land areas. Near the townsite of Frankfort, fossil leaves from rocks of unit III were identified by J. A. Wolfe as representing five genera: Fagus, Metasequoia, Quercus, Sequoia, and Vitis (E. J. Moore, in litt.). Farther east, near Rocky Point, plant fossils are abundant. From this locality J. A. Wolfe identified twelve taxa, including the genera Cercidiphyllum, Metasequoia, Osmunda, and Quercus. Rocks of unit III were deposited in part by turbidity currents at depths ranging from 16 to 650 meters (Wolfe and McKee 1972:51, 54).

In summary, the new taxon lived in a relatively

Table 1

Decapod crustacean diversity: Astoria Formation of southwestern Washington. (Unit divisions follow Wolfe and McKee 1968, 1972.)

Genus and Species	Unit I	Unit II	Unit III
Turalua ancience an 1	x		x ²
Mursia yaavinansia	v	v	
Callianassa alallamansis			
Callianassa tuinansis n-m			v v
Cancer wahliakumensis y <=	X	x	
Cancer sp. $(2 \text{ other species})^1$			t
Cancer sp. $(1 \text{ species})^1$			X
Munida sp. ¹	x		
Macrocheira cf. M. teglandi		X	
Undetermined genera (2) ³		x	

1. Undetermined species, possibly new.

2. Specimen may have been derived from Unit I sediments, locality being

adjacent to contact between Units I and III.

3. Possibly new genera.

small early Miocene embayment, with a substrate that ranged from muddy to sandy and usually contained organic detritus. This embayment was near the mouth of a large river, the water was warm, and the climate was subtropical.

MATERIALS AND METHODS

The authors collected from every outcrop of the Astoria Formation that could be found in the Naselle– Grays River area from about 1980 to 1990 (fig. 1). All outcrops along major stream and river channels were prospected for fossils; every decapod fossil that appeared to be diagnostic was collected.

These institutional acronyms are used for specimen and locality numbers: UWBM (Thomas Burke Memorial Washington State Museum, University of Washington, Seattle, Washington); LACMIP (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section, Los Angeles, California); USNM (United States National Museum of Natural History, Washington, D.C.); NP (Leland Stanford Junior University, Stanford, California).

Voucher specimens of callianassid shrimps from the Astoria Formation in the Naselle, Washington, vicinity are: Callianassa clallamensis UWBM 11829, from locality UWBM B5680; C. twinensis UWBM 11827, locality UWBM B5679; and C. twinensis UWBM 11828, locality UWBM B5680. Other fossil decapods mentioned are under study by Berglund.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1803 Infraorder BRACHYURA Latreille, 1803 Section CANCRIDEA Latreille, 1803 Family CANCRIDAE Latreille, 1803 Subfamily CANCRINAE Latreille, 1803 Genus Cancer Linnaeus, 1758

Included subgenera: Cancer (Linnaeus, 1758); Glebocarcinus Nations, 1975; Metacarcinus (Milne-Edwards, 1862); Romaleon (Gistl, 1848). Subgenus Romaleon (Gistl, 1848) Cancer (Romaleon) wahkiakumensis, new species, figs. 2–16

Diagnosis

Crab small. Carapace broad, with 8 sharp-tipped anterolateral teeth having finely granulated margins; carapace widest at 8th anterolateral tooth; front moderately produced with 5 frontal teeth; medial tooth narrow, short, subacute; inner orbital tooth very small, tip rounded; outer orbital tooth long, acute; posterolateral margins strongly concave, without teeth or carinae. Chelipeds equal in size; movable fingers and mani with three sharp spines on thin upper margins; outer surface of mani carinate.

Description

Carapace suboctagonal, wider than long; moderately arched longitudinally, less so transversely; 8 anterolateral teeth, including outer orbital tooth and tooth at posterolateral angle; carapace widest at 8th anterolateral tooth, nearly as wide at 7th anterolateral tooth. Length from tip of medial tooth to posterior margin approximately 70% maximum carapace width; distance from frontal margin posterior to line indicating maximum carapace width approximately 70% total length. Posterolateral margins concave in outline; posterior margin narrow, approximately 30% maximum carapace width. Fronto-orbital width nearly 40% maximum width; anterior extension of front produced slightly more than orbits. Orbits moderately large, elliptical, with two deep, longitudinally-trending fissures in supraorbital margin. Medial tooth, and 2 adjoining teeth, blunt to subacute, approximately equal in anterior extension; medial tooth much narrower and shorter than adjoining pair, contiguous with narrow anterior portion of the mesogastric region. Inner orbital teeth very small, short and narrow, with rounded nipple-like tips, on same vertical plane as three medial teeth, with anterad extension not as great; each inner orbital tooth separated from tooth on axial side by broad, shallow sinus. On supraorbital margin, just posterior to inner orbital tooth, a much larger tooth with subacute tip; on abaxial side of this larger tooth, supraorbital margin concave to first of 2 deep, closed fissures parallel to the main axis; orbital tooth broadly rectangular, its anterior margin transverse and rimmed with small, bead-like granules. Anterolateral teeth sharp-tipped and triangular in shape; teeth 1 through 6 anteriorly directed, 7 anterolaterally directed, 8

Figures 2-7. Cancer wahkiakumensis, new species.

- Fig. 2. Holotype, UWBM 74400: carapace, dorsal view, x 1.2
- Fig. 3. Holotype, UWBM 74400: chelipeds, outer view, x 1.2
- Fig. 4. Paratype, USNM 448195: ventral view, abdomen and sternum, x 1.6
- Fig. 5. Paratype, LACMIP 8284: carapace, dorsal view, x 1
- Fig. 6. Referred specimen, LACMIP 8287: carapace, dorsal view, x 1.5
- Fig. 7. Paratype, UWBM 74404: right cheliped, inside view, x 1.75





laterally directed. Cross-sections at bases of teeth 1 through 7 elliptical, at tips circular; tooth 8 circular from base to tip. All anterolateral teeth separated to their bases, edges finely granulate; outer margins of teeth 1 through 7 straight; between teeth are deep rounded sinuses, shallowest between teeth 3 and 4, deepest between teeth 6, 7, and 8. No teeth or carinae on posterior or posterolateral margins.

Carapace surface moderately to sharply differentiated into elevated regions. Gastric, cardiac, and branchial regions moderately inflated; mesogastric, urogastric, and cardiac regions weakly demarcated; epibranchial region and anterior end of elongated branchial lobes prominently swollen; metabranchial region with small node. Interregional furrows well defined; 3 prominent furrows project posteriorly from sinuses in frontal margin; in mesobranchial and gastrocardiac regions furrows very deeply incised. Entire surface of carapace covered with dense network of fine granules; a few large granules scattered over surface of mesogastric and metagastric regions; several large tubercles on metabranchial and mesobranchial regions.

Abdomen of male composed of 6 somites: somites 1 through 4 shortest; 1 through 3 approximately equal in width; sides of somite 3 narrowing anteriorly, 4 and 5 nearly parallel, those of somite 6 converging to a sharp tip.

Walking legs: meri long, thin, nearly equal in length, locally thickened at distal ends near articulation with carpus; carpus of last walking leg long, upper margin very convex, lower concave, distal end subtriangular in cross-section. Carpus, and parts distal to the merus, appear to have been posteriorly directed.

Chelipeds equal; manus long, high distally, upper and lower margins strongly convergent proximally, outer surface gently convex longitudinally, strongly convex vertically, vertical cross-section through hand narrowly diamond-shaped, elongate vertically. Outer surface of hand carinate; upper margin (carina 1) thin and bladelike with 3 sharp, distally-inclined spines equally spaced between distal angle and upper articulation with carpus; largest spine at distal angle, smallest spine low and weakly defined near articulation. Outer-upper surface convex, coarsely granulate to scabrous near upper margin, coarsely reticulate closer to the median. Three

inconspicuous carinae on this surface indicated by alignments of decorative features approximately equally spaced; an irregular longitudinal row of large granule groupings (carina 2) immediately below the upper margin; 2 uneven rows formed by aligned sections of the reticulate pattern (carinae 3 and 4), converging distally, nearly meeting at articulation. Carina 5 a well defined ridge on the median, extending full length of hand; carina 6 is a prominent raised and broadly rounded rim along lower margin extending from lower articulation with carpus to tip of fixed finger. Surface between carinae 5 and 6 relatively smooth. Inner surface of manus concave longitudinally, convex vertically, with a prominent carina along the median; surface with scattering of fine granules. Length of merus approximately that of manus, width at mid-length approximately twice that at articulation with ischium. Upper surface of carpus bordered by narrow band of granules beginning near upper articulation with manus and extending distally to base of large, sharp, distally directed spine at upper distal angle; at inner angle, a much shorter spine. Subparallel to proximal half of upper surface on ridge, 2 or 3 short longitudinal carinae with several transverse ridges; entire area finely granulate. Large, sharp, conical tubercle located adjacent to upper articulation, one of four tubercles forming an irregular diagonal carina.

Fixed fingers acutely triangular in shape; inner surface smooth, gently concave longitudinally; outer surface with 2 narrow, longitudinal grooves, dividing finger into 2 low ridges, one bordering lower margin of finger, the uppermost separated from bases of cutting teeth by narrow, shallow groove. Four or 5 large, oval, setal pits; several small, circular depressions along bases of cutting teeth; tip of each tooth darkened. Both leftand right-hand fixed fingers have 11 cutting teeth, differing slightly in size and position. Right-hand fixed finger with teeth 1, 2, 3, 5, 6, 8, 9, and 11 small, subequal, with some darkening on each; teeth 4, 7, and 10 large, size increasing distally, 50-75% of each tooth darkened; teeth 4 and 7 subacute; tooth 10 very long, narrow, acute. Left-hand fixed finger with teeth 1, 2, 3, 4, 6, 7, 9, and 11 small, subequal in size, with some darkening on each; teeth 5, 8, and 10 large, size increasing distally, 50-75% of each tooth darkened; teeth 5 and 8 subacute; tooth 10 very long, narrow, acute.

Figures 8-14. Cancer wahkiakumensis, new species.

- Fig. 8. Paratype, UWBM 74403: right merus and carpus of fifth leg, x 1.75
- Fig. 9. Paratype, USNM 448194: left cheliped, outer view, x 2.75

Fig. 10. Paratype, USNM 448194: carapace, dorsal view, x 2.8

- Fig. 11. Paratype, LACMIP 8286: left cheliped, outer view, x 1.5
- Fig. 12. Paratype, LACMIP 8285: carapace, front view, x 1

Fig. 13. Paratype, USNM 448194: carapace, front view, x 2.4

Fig. 14. Paratype, UWBM 74403: chelipeds, outer view, x 1.6

Movable fingers thin; upper margin very highly arched, highest section approximately at mid-length, proximal one-third nearly at right angle to distal onethird. Three long, distally inclined spines equally spaced along middle one-third of upper margin; proximal spine largest, distal spine smallest. Outer surface slightly convex longitudinally and transversely; granules scattered along crest between spines; punctae small, densest on upper one-third, scarce near toothline; several setal pits along baseline of teeth; tip of each finger darkened. Both left- and right-hand fingers with 8 cutting teeth, some variation in tooth size and location. Righthand finger with first tooth large, conical, inclined toward articulation with hand, half of tip darkened; teeth 2, 3, and 4 small; tooth 5 large, acute; teeth 6, 7, and 8 long, occlusal surfaces nearly flat, thin, ridge-like. Distal one-fifth of occlusal surface without teeth. Left-hand



Figure 15. *Cancer wahkiakumensis*, new species: reconstruction of carapace showing location and orientation for measurements in table 2.

Table 2

Carapace measurements (in mm) for *Cancer wahkiakumensis* **n. sp.** (See fig. 15 for location and orientation of measurements.) finger with teeth 1 through 5 small, with some darkening on each; tooth 6 large, acute, one-half of tip darkened; teeth 7 and 8 low, elongate; distal one-fifth of occlusal surface ridge-like, without teeth.

Measurements (in mm)

Carapace measurements are listed in table 2; their orientation and location are shown in figure 15. Cheliped measurements (table 3) were made at locations specified by Nations (1975: fig. 3). Several selected pairs of cheliped measurements have been combined as ratios in table 4 following the system used by Nations (1975: 8).

Etymology

The new species is named for Wahkiakum County, Washington, wherein the holotype was collected.

Material

HOLOTYPE: UWBM 74400 (locality UWBM B5497). PARATYPES: UWBM 74401, 74402 (locality UWBM B5498); UWBM 74403, 74404, 74405, 74406 (locality UWBM B5500); USNM 448194 (locality UWBM B5499), USNM 448195 (locality UWBM B5500); LACMIP 8284, 8285, 8286 (locality LACMIP 5848), LACMIP 8289, 8290 (locality LACMIP 5848), LACMIP 8291 (locality LACMIP 5847). PLASTOHOLOTYPES: LACMIP 8282, USNM 448496. PLASTOPARATYPE: LACMIP 8283 (cast of USNM 448194). Referred specimens, UWBM 74407 (locality UWBM B5497), UWBM 74408 (locality UWBM B5500), LACMIP 8287 (locality LACMIP 12218), LACMIP 8288, 8292 (locality LACMIP 5864), LACMIP 8293 (locality LACMIP 5848).

Occurrence

Type locality, UWBM B5497, Astoria Formation (Unit II), Wahkiakum County, Washington. Unit I (Naselle unit), UWBM locality B5498 (=LACMIP loc. 12218), LACMIP loc. 5847, LACMIP loc. 5864, all in Pacific County, Washington; Unit II, UWBM localities B5499, and B5500 (=LACMIP loc. 5848) in Wahkiakum

Specimen	W/1	L/1	F	W/2	L/2
UWBM 74400	62.3	40.7	24.3	17.0	27.0
USNM 448194	30.0	20.7	14.0	8.8	14.1
LACMIP 8289	45.6	33.0	17.6	9.8	22.0
LACMIP 8290		21.0	13.5	8.0	14.0

County. Precise locality descriptions are available upon request to the appropriate institution.



Figure 16. *Cancer wahkiakumensis*, new species: reconstruction of left chela (articulation with carpus not shown).

Table 3

Cheliped measurements (in mm) for *Cancer* wahkiakumensis, n. sp.

Specimen	Manus Lu	Hm	Fixed F Lf	inger Hf	Movab Lmf	le Finger Hmf
UWBM 74403	20.2L	15.0L	12.6L	6.3L, 6.2R	17.6L	5.4L
UWBM 74404	1	15.7R	11.7R	5.8R		
LACMIP 8286		12.5L		5.0L		4.2L
UWBM 74406			16.0R	8.0R		
USNM 448194	10.5L	8.3L	6.2L	3.4L	9.0L	3.0L

Lu – Length, upper margin of manus; Hm – height of manus; Lf – length, fixed finger; Hf – Height, fixed finger; Lrmf – length, movable finger; Hmf – height, movable finger; L – left; R – right.

Table 4

Cheliped ratios (follows Nations 1975). (See Table 3 for key to abbreviations.)

Discussion

The new crab, *Cancer wahkiakumensis*, is superficially similar to species within the family Portunidae in having a carapace with eight anterolateral teeth and lacking posterolateral protuberances and carinae; however, some characters diagnostic of Portunidae (e.g., branchial ridging and swimming legs) are absent. The new taxon resembles more closely the family Cancridae, especially species of the genus *Cancer*, in the shape and spination of the carapace and chelipeds, the shape of the anterolateral teeth, and the shape and dentition of the front; however, the carapace differs from that of all other species of *Cancer* (in which the carapace is known) by lacking posterolateral teeth and carinae, and by having only eight anterolateral teeth.

The chelipeds of all previously described species of *Cancer* have mani with six or seven longitudinal carinae on the outer surface (Nations 1975). The mani of C. *wahkiakumensis* have six carinae (fig. 16), although

carinae 2, 3, and 4 are represented by inconspicuous rows of decorative elements, best preserved on paratype UWBM 74403, and faintly discernible on paratype USNM 448194.

Nations (1975) reviewed the genus Cancer, including all known Recent species and all extinct species from western North and South America, and recognized four subgenera: Cancer, Glebocarcinus, Metacarcinus, and Romaleon. The carapace of Cancer wahkiakumensis lacks the ornate areolation

and strong differentiation of regions possessed by species of the subgenus *Glebocarcinus*. Species of the subgenera *Cancer* and *Metacarcinus* have ovate carapaces with truncate anterolateral teeth, whereas the carapace of *C. wahkiakumensis* is suboctagonal with sharp-tipped, forward pointing anterolateral teeth. Based primarily on carapace morphology, *C. wahkiakumensis* appears to be most closely related to species of the

> subgenus Romaleon. Of the ten species of the subgenus Romaleon recognized by Nations (1975), Cancer wahkiakumensis most closely resembles C. gibbosulus Rathbun, 1898; C. branneri Rathbun, 1926; and C. dereki Nations, 1975. Cancer gibbosulus is a Recent species which lives along the coasts of Japan and China in the western Pacific Ocean; C. branneri ranges

Specimen	Lu/Hm	Hf/Hm	Hf/Lf	Hmf/Lmf
UWBM 74403 (L)	1.347	0.420	0.500	0.307
UWBM 74404 (R)		0.369	0.496	
LACMIP 8286 (R)		0.400		
UWBM 74406 (R)		0.500		
USNM 448194 (L)	1.265	0.409	0.548	0.330
Average (L)	1.306	0.414	0.524	0.318
(R)		0.423	0.496	

from Pliocene in California to Recent in the eastern North Pacific Ocean from California to Alaska; and C. dereki is known only from middle Miocene-age rocks in California. All three have an anterolateral tooth shape and orientation that is similar to that of C. wahkiakumensis, but they differ from C. wahkiakumensis by having an alternation in tooth size in which the oddnumbered teeth are larger, and the even-numbered ones are smaller. The last anterolateral tooth of C. branneri is directed anteriorly, not transversely outward as in C. gibbosulus, C. dereki, and C. wahkiakumensis. The deep furrows extending posteriorly from the sinuses in the anterior margin of the carapace of C. wahkiakumensis are comparable to those of C. dereki, to a lesser degree to those of C. gibbosulus, and even less to those of C. branneri. For both C. wahkiakumensis and C. dereki, outline and areolation of the carapace, and shape and orientation of the anterolateral teeth, are similar; however, decoration along tooth margins of C. wahkiakumensis is a fine granulation instead of spinules. The carapace width of both species is widest between the tips of the teeth at the posterolateral angles. The carapace of C. wahkiakumensis differs from that of all other species of *Romaleon* in being much less ovate in outline. The carapace of C. yanceyi Nations, 1975, is unknown and the species is based on two fossil mani. The manus of C. yanceyi is short, with seven carinae on the outer surface, whereas that of C. wahkiakumensis is long, with six carinae on the outer surface.

Although *Cancer wahkiakumensis* possesses several unique characters that are not shared by any other known species of *Cancer*, these are not considered sufficient at this time to justify the naming of a new genus. The discovery of better preserved and more complete specimens, as well as the description of other new taxa from western North America (see Feldmann, Tucker, and Berglund 1991), may indicate the need for recognition of a new genus.

Except for an undescribed species of *Cancer* from the late Eocene Hoko River Formation (Feldmann, Tucker, and Berglund 1991), *Cancer wahkiakumensis* is the earliest record of the genus *Cancer* in the eastern Pacific Ocean; all other species of *Cancer* are middle Miocene age or younger (Nations 1975). Because it is known only from rocks within one small Miocene-age embayment, *C. wahkiakumensis* may have been endemic to that embayment.

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